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Potential for maternal effects on offspring CO_2 sensitivities in the Atlantic silverside (*Menidia menidia*)

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ABSTRACT

For marine fish, the influence of maternal provisioning on offspring sensitivity to high carbon dioxide (CO_2) conditions remains unknown. We separately reared offspring obtained from five wild-caught Atlantic silverside (*Menidia menidia*) females from fertilization to 16 days post hatch under contrasting CO_2 conditions (ambient: ~400 μatm, acidified: ~2,300 μatm), testing whether average survival during the embryo and larval stage, hatch length, final length, and growth rates were affected by CO_2, female identity, or their interaction. Average trait responses did not significantly differ between treatments (CO_2 or female identity), however, significant CO_2 × female identity interactions indicated that females produced offspring with different average CO_2 sensitivities. We then examined whether differential egg provisioning with fatty acids (FA) may partially explain the observed differences in offspring CO_2 sensitivities. Concentrations of 27 FAs in the unfertilized eggs of each female were measured. Cumulative absolute FA levels were negatively related to hatch length and to the log-transformed CO_2 response ratio of hatch length. Eggs with lower concentrations of 20:1*n*9 and 22:5*n*3 resulted in offspring where embryo survival was negatively impacted by high CO_2. Eggs with higher concentrations of 18:3*n*3, 18:4*n*3, and 22:6*n*3 produced shorter offspring at hatching under high CO_2 conditions. These results indicate that maternal provisioning might be an additional determinant of CO_2 sensitivity in fish early life stages. Acidification experiments should therefore utilize large numbers of parents from different natural conditions and, where possible, track heritage.

1. Introduction

The extent to which offspring fitness is determined by gene × environment interactions as well as non-genetic parental effects comprises a long-standing research topic in biology (Bernardo, 1996). Maternal effects, where mothers influence offspring fitness via propagule provisioning (Andree et al., 2015; Chambers and Leggett, 1996; Mousseau and Fox, 1998), mate-choice and behavior (Green and McCormick, 2005; Trippel et al., 2005), and transgenerational epigenetic inheritance (Jablonka and Raz, 2009; Räsänen and Kruuk, 2007; Salinas et al., 2013), appear to be ubiquitous across taxa. Maternal effects have important implications in a number of fields, including fisheries, where adequate recruitment likely depends on preserving the age structures in commercial fish stocks because older females produce larger, energy-enriched, and more viable eggs (Berkeley et al., 2004; Johnston and Leggett, 2002; Marteinsdóttir and Steinarsson, 1998; Trippel et al., 2005). Likewise, evaluating climate change impacts on species, populations, and ecosystems requires knowledge of maternal effects because they may obscure or exaggerate responses of individuals to environmental change including ocean warming and acidification (Munday, 2014).

Ocean acidification, which is part of the larger syndrome of marine climate change (Doney et al., 2009; Pörtner, 2012), has rapidly emerged as a major research topic over the past two decades (Browman, 2016; Busch et al., 2015). Experimental approaches have played a prominent role as a necessary first step to distinguish CO_2 sensitive from CO_2 tolerant marine taxa as well as life-stages and individual trait responses within taxa. To date, the majority of empirical data suggest negative responses to high CO_2 (Harvey et al., 2013; Hendriks et al., 2010; Kroeker et al., 2010; Kroeker et al., 2013), with calcifying invertebrates and early life stages of marine species being the most vulnerable (Baumann et al., 2012; Bednaršek et al., 2014; Kleypas et al., 2006; Waldbusser et al., 2013). However, there is also increasing evidence for non-linear (Ries et al., 2009), neutral (Hurst et al., 2013), and even positive effects of elevated CO_2 exposures (Gooding et al., 2009; Schade et al., 2014) within many of the traits or taxa examined to date, thereby precluding simple answers and generalizations (Browman, 2016; Busch et al., 2015).

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Despite the strong likelihood of maternal environments and conditions affecting offspring development (Chambers and Leggett, 1996; Donelson et al., 2008; Gagliano and McCormick, 2007; Green, 2008), little has been done to investigate this in ocean acidification experiments, particularly in those that rely on progeny from a limited number of parents (Chambers et al., 2014; Frommel et al., 2012a; Hurst et al., 2013), which have been maintained in captivity prior to their use as a source of offspring. Studies assessing cross-generational CO_2 responses have suggested that parental exposure to high CO_2 either mitigated or neutralized offspring CO_2 sensitivity for some traits, e.g., in Sydney rock oyster (*Saccostrea glomerata*, Parker et al., 2012) or clown fish (*Amphiprion melanopus*, Allan et al., 2014; Miller et al., 2012), while having little or even adverse effects in other species or traits (Griffith and Gobler, 2017; Welch et al., 2014). In the Atlantic silverside (*Menidia menidia*, Atherinopsidae), offspring tolerance to high CO_2 increases seasonally while fish are spawning in late spring to summer months, suggesting transgenerational acclimation as a possible explanation (Murray et al., 2014).

Here we explored whether maternal provisioning can influence offspring CO_2 sensitivity, using *M. menidia* as a model. Given their ecological importance as forage fish and the relative ease of laboratory manipulation, members of the silverside family have become frequent temperate fish models in ocean acidification research (Baumann et al., 2012; Depasquale et al., 2015; Lopes et al., 2016; Malvezzi et al., 2015; Miller et al., 2016; Murray et al., 2017). In addition, maternal and genetic effects on offspring size have previously been demonstrated in this species (Bengtson et al., 1987; Gao and Munch, 2013). Here, wild-caught adults were spawned to test whether offspring from different mothers differ in their average survival and growth responses to elevated CO_2 conditions. Differences in embryonic and larval responses were evaluated for differential provisioning of eggs with fatty acids (FAs). Variations in FA profiles have previously been shown to affect larval fish performance (Fuiman and Ojanguren, 2011) and are likely implicated in metabolic programming (Fuiman and Perez, 2015). As recently demonstrated, FA levels in larval fish can also vary in response to different CO_2 exposures (Díaz-Gil et al., 2015). We thus assumed that FA profiles would afford a more detailed look into the potential relationship between maternal provisioning and offspring CO_2 sensitivity than proxies like egg size (Stephens et al., 2009) or mass (Johnston and Leggett, 2002), which are relatively invariant and unrelated to maternal size in this species (Bengtson et al., 1987).

2. Materials and methods

2.1. Sampling and experimental design

Adult silversides were collected by beach seine (30 × 2-m, 3-mm mesh) at Mumford Cove, Connecticut (41.32°N, 72.02°W) on 1 June 2016, approximately a fortnight after their May full moon spawning peak. Spawners were transported live to the Rankin laboratory (University of Connecticut) and held overnight in aerated 60-l tanks at 20 °C to promote egg hydration. The following day, five randomly selected females were strip-spawned onto cutout sections of window screen (1-mm mesh) that were placed into separate seawater-filled spawning dishes (Murray et al., 2014). To ensure full fertilization success and randomize potential paternal effects, eggs were fertilized with a mixture of milt from 22 males, thus producing full-sib and maternal half-sib embryos from each female. Adults were measured for total length (TL; mean TL_{male} = 9.14 cm, mean TL_{female} = 10.4 cm) and frozen for later analysis of FA. Mesh screens with attached embryos were subsequently cut into smaller sections to allow precise enumeration, and within 2-h post-fertilization 100 embryos were placed into each of three replicate rearing containers (20 l) per female and CO_2 treatment (i.e., 600 embryos for each of five females, 3 × 100 in ambient and 3 × 100 in acidified treatments). Rearing containers were filled with 1-μm filtered, UV-sterilized seawater (~30 psu) from Long Island Sound and placed in temperature-controlled water baths set to 24 °C, the known thermal optimum for survival and growth in this species (Middaugh et al., 1987). Offspring were reared for 24 d post fertilization under a 15 h light:9 h dark lighting regime. After hatch, larvae were fed ad libitum rations of newly hatched brine shrimp nauplii *Artemia salina* (brineshrimpdirect.com), and 50% of water was replaced every 5 d to ensure safe ammonia levels (< 0.25 ppm). Hatched larvae were counted and subsampled (n = 10 per replicate) at 1 d post hatch (dph) by gently scooping them into identical 20 l containers, and final samples were taken at 16 dph. All samples were preserved in 10% buffered formalin for later measurements of larval standard length (SL, 0.01 mm) via calibrated digital images (ImagePro Premier, MediaCybernetics). The experiment thus quantified three related survival and three size traits for each replicate, female, and CO_2 treatment: embryo survival (fertilization to 1 dph), larval survival (1 to 16 dph), overall survival (fertilization to 16 dph), size (SL) at hatch (1 dph), SL at 16 dph, and larval growth rate (GR = (SL_{16dph} − SL_{1dph}) / 15).

2.2. CO_2 regime

Offspring were reared at ambient (~400 μatm, pH_{NBS} = 8.18) and acidified CO_2 conditions (~2300 μatm, pH_{NBS} = 7.50). The higher value was set to a level commonly used in OA research (consistent with projections of future pCO_2 values for open oceans over the next 200 yr (IPCC, 2007)) and represents current conditions experienced during seasonal extremes by this species in nature (Murray et al., 2014). Ambient conditions were achieved by bubbling partially CO_2-stripped air into each rearing container, thereby offsetting metabolic CO_2 accumulation. Acidified conditions were achieved via gas proportioners (Cole Parmer®) that mixed CO_2 stripped air with 100% bone-dry CO_2 delivered to the bottom of each rearing container via air stones. Target pH and temperature were monitored daily via a handheld pH probe (Hach® HQ40d portable meter with a PHC201 standard pH-probe) calibrated regularly via two-point National Bureau of Standards (NBS) pH buffers (electronic supplementary material, Fig. S1). To characterize actual pCO_2 levels and related water chemistry parameters, water was sampled from four randomly chosen rearing containers per treatment three times over the course of the experiment and immediately measured for total alkalinity (A_T) via endpoint titration (Mettler Toledo™ G20 Potentiometric Titrator). The instrument has previously been shown to quantify A_T in Dr. Andrew Dickson's reference material (batch 147, A_T = 2231.39 μmol kg seawater^{-1}) with an average error of 0.6%. Actual levels of total dissolved inorganic carbon (C_T), partial pressure of CO_2 (pCO_2), fugacity of CO_2 (fCO_2), and carbonate ion concentration were calculated in CO2SYS (http://cdiac.ornl.gov/ftp/co2sys) based on measured A_T, pH (NBS), temperature, and salinity

Table 1
Overview of experimental conditions and carbon chemistry. Mean (± SD) pH_{NBS} and temperature (°C) were derived from daily measurements, while mean (± SD) total alkalinity (A_T; μmol kg^{-1}) was measured via endpoint titration from three random seawater samplings during the experiment. Dissolved inorganic carbon (C_T; μmol kg^{-1}), partial pressure of CO_2 (pCO_2; μatm), fugacity of CO_2 (fCO_2; μatm), and carbonate ion concentration (CO_3^{2-}; μmol kg^{-1}) were calculated in CO2SYS.

CO_2	$pH_{(NBS)}$	Temp	A_T	C_T	pCO_2	fCO_2	CO_3^{2-}
Ambient	8.18 ± 0.12	23.28 ± 0.22	2189.09 ± 13.34	1945.79 ± 12.29	403.64 ± 2.55	402.33 ± 2.54	178.18 ± 1.13
High	7.50 ± 0.11	23.57 ± 0.38	2188.24 ± 24.56	2193.44 ± 24.83	2290.11 ± 25.93	2282.72 ± 25.84	44.13 ± 0.50

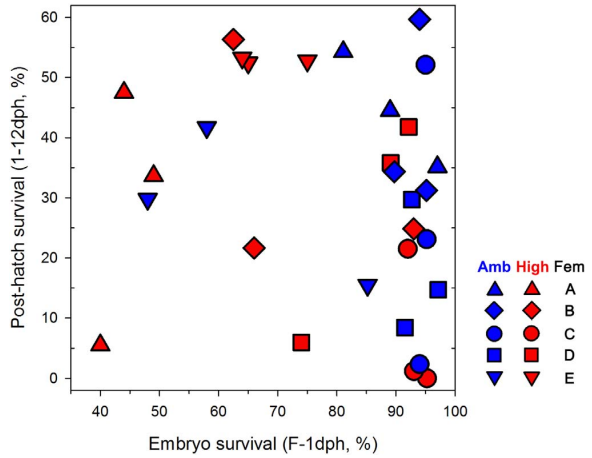

Fig. 1. *M. menidia.* Relationship between larval survival (1 dph to 16 dph, %) and embryonic survival (fertilization to 1 dph, %) of offspring from five different females (A–E) reared at ambient (blue symbols) and high (red symbols) CO_2 levels. Points represent individual replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using K1 and K2 constants from Mehrbach et al. (1973) refit by Dickson and Millero (1987) and Dickson (1990) for $KHSO_4$ (Table 1).

2.3. Fatty acid analysis

Gas chromatography was used to quantify the absolute (mg g dry-weight^{-1}) and relative concentrations (% of total) of 27 FAs for each of the 5 females (whole individual) and their unfertilized eggs (~1 ml) following the methods of Faulk and Holt (2005) as recently used for this species in Murray et al. (2017). Briefly, frozen samples were shipped on dry ice to the Fisheries and Mariculture Laboratory (University of Texas, Marine Science Institute), where they were first dried and then homogenized in a solution of chloroform-methanol (2:1 v/v) and tricosanoic acid (23:0) as an internal standard for quantification of mg g^{-1} dry mass of fatty acids. Lipids were cold-extracted from approximately 50 mg of dry mass. Fatty-acid methyl esters were prepared by saponification in potassium hydroxide, followed by transesterification with 14% boron trifluoride in methanol. A Shimadzu GC-2014 gas chromatograph set with a Phenomenex ZB-WAX plus capillary column (30 m long; 0.53 mm ID; 1.0 μm thick) was used to quantify FAs, and individual FAs were identified by comparison to commercial standards (Supelco, Inc.). Two FAs, 12:0 and 15:1, were below detection limit or invariant across egg batches and were therefore excluded from subsequent analyses.

2.4. Data analysis

Pearson bivariate correlation analysis was used to test whether embryonic and larval survival rates were related within each CO_2 treatment. Next, multivariate analysis of variance (MANOVA) was used to test for overall effects of female identity, CO_2 treatment (fixed factors) and their interaction on embryonic and larval survival (S), whereas the derived variable 'overall survival' was not included in the model. The MANOVA model had the form.

$$S = CO_2 + \text{female} + CO_2{*}\text{female} + \varepsilon(\text{error}).$$

A logit transformation $[= \log_{10}(S / (1 - S))]$ was applied to survival proportions prior to statistical analysis. Significance was tested using Pillai's trace, the most conservative of commonly used MANOVA test statistics. MANOVA was then followed by ANOVA of the same design to test for CO_2, female, and interaction effects on each survival measure separately. In a similar manner, MANOVA followed by ANOVA was used to test for overall and separate effects, respectively, of CO_2, female, and their interaction on the two size traits (i.e., hatch SL and final SL; growth was excluded). Unweighted averages were used for hatch SL and final SL. For each trait, five *t*-tests were computed to examine treatment differences within each female, using a Bonferroni adjustment ($\alpha/5 = 0.01$) to reduce the likelihood of Type I errors. All groups were tested for a normal distribution via Shapiro-Wilk and variance homogeneity using a Levene's test. To characterize the average sensitivity to elevated CO_2 for each of the five offspring sets and enable comparisons to FA provisioning, the log-transformed CO_2 response ratio (lnRR) was calculated for each trait (T) as $\text{lnRR(T)} = \ln(T_{high}) - \ln(T_{ambient})$ using replicate averages for each T. LnRRs are common metrics in meta-analyses, because they quantify the proportional change resulting from experimental manipulations, have robust statistical properties, and a straightforward biological interpretation (Hedges et al., 1999; Kroeker et al., 2010). Negative lnRRs would be indicative of a reduction in trait value at high compared to ambient CO_2 levels.

FA profiles of females and their unfertilized eggs were first used to calculate FA-specific (mg g^{-1} dw) and overall egg enrichment factors ($E = FA_{egg} / FA_{fem}$), which were then correlated to each lnRR(T) using Pearson bivariate correlation analysis. Secondly, the cumulative absolute FA content was calculated for each egg batch as the sum of all FAs measured, which was then correlated to each lnRR(T) using Pearson bivariate correlation analysis. To explore whether specific FAs in eggs affected the CO_2 sensitivity of resulting offspring traits, we first performed principal component analysis on absolute FA concentrations (mg dw g^{-1}) and subsequently identified specific FAs that had high loadings (> 0.85) on any of the first three principal components (i.e., those with eigenvalues > 1). For this specific subset of FAs, we then used linear regression to relate absolute FA concentration to lnRR(T). All statistical analyses were computed using SPSS (V20, IBM).

3. Results

3.1. Offspring survival

Survival during the embryo and larval stages ranged from 40.0 to 94.1% and 0.0 to 59.9%, respectively. Considering all replicates per treatment, average (± SD) embryo survival at ambient and acidified conditions was 86.8 ± 14.6% and 72.9 ± 7.7%, whereas larval survival was 31.8 ± 14.6% and 30.3 ± 25.2%, respectively. There was no significant correlation between embryo and larval survival in ambient or acidified treatments (Pearson correlation, $P = 0.3$, Fig. 1). Variability among replicates was high; at ambient CO_2 conditions, the average standard deviation of embryo, larval, and overall survival was 14.5%, 17.0%, and 15.4%, respectively, compared to 19.1%, 20.4%, and 14.0%, respectively, at high CO_2 conditions. Across both survival measures, MANOVA identified significant overall effects of female ($P = 0.002$), CO_2 ($P = 0.002$), and female * CO_2 ($P = 0.026$), the latter indicating that some females produced offspring with divergent average CO_2 sensitivities with respect to survival (Fig. 2A,B, Table 2). Univariate ANOVAs indicated that the majority of these effects were driven by differences in survival during the embryonic stage ($P < 0.03$ for female, CO_2, and their interaction), not during the larval stage (Table 3). Offspring from three females showed some degree of average reduction in embryonic survival at high compared to ambient CO_2 conditions, but only one female (female A) showed a difference that was significant (*t*-test, $P = 0.004$). Overall survival at high compared to ambient CO_2 conditions was reduced for offspring of female A ($P = 0.01$), but slightly increased for offspring of female E ($P = 0.013$, non-significant after Bonferroni correction, Fig. 2A,B).

3.2. Offspring size

Considering all replicates, average (± SD) hatch and larval SL were

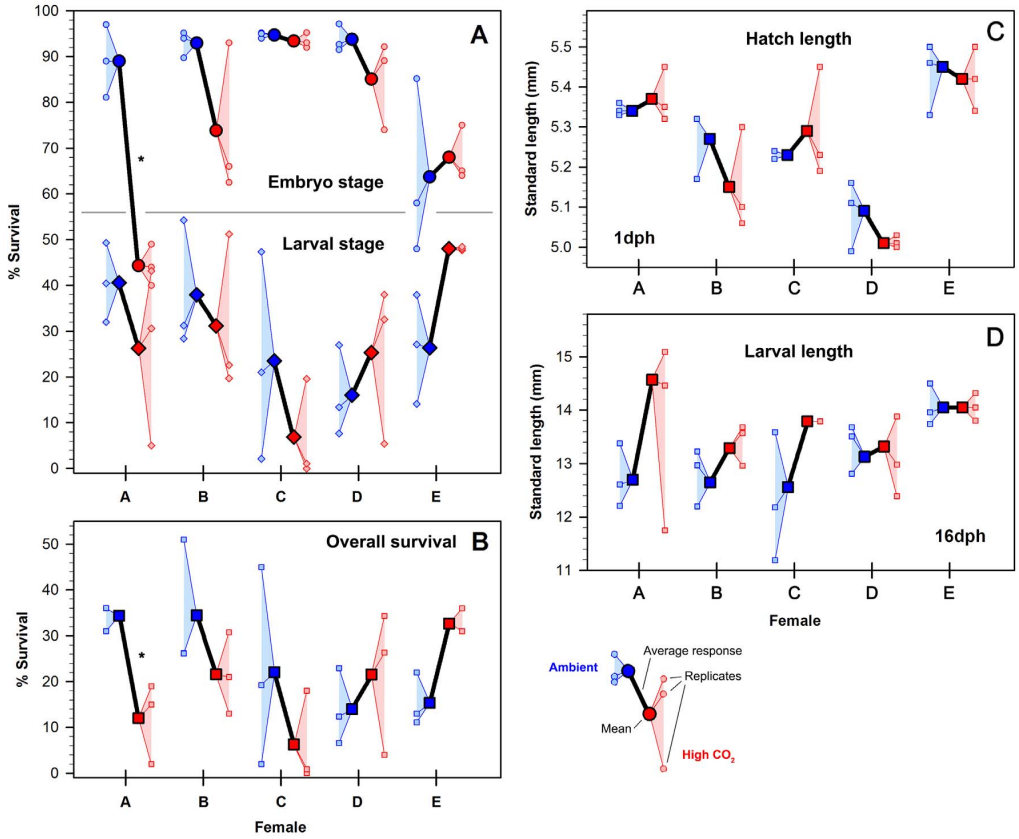

Fig. 2. *M. menidia*. Responses to high CO_2 conditions among replicates within and among females: (A) embryo and larval survival; (B) overall survival; (C) SL at hatch; and (D) final SL (16 dph). Patterns of larval growth were nearly identical to panel D and are therefore omitted. Ambient and high CO_2 treatments are denoted by blue and red colors, respectively. Small symbols depict replicate survival (A,B) or replicate average size (C,D), while large symbols depict CO_2 treatment averages for each female. Black lines connect average response for each female. Asterisks represent significant differences ($P < 0.05$) between CO_2 levels within offspring of each female (Bonferroni adjusted *t*-test). Letters denote to females A to E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
MANOVA testing for effects of female, CO_2, and their interaction on combined *M. menidia* offspring survival (i.e., logit-transformed embryo and larval survival,) using Pillai's Trace test statistic.

Effect	F	Hypothesis df	Error df	P
Female	3.82	8	40	**0.002**
CO_2	8.51	2	19	**0.002**
Female ∗ CO_2	2.51	8	40	**0.026**

Bolded P-values are significant at the 0.05 level.

Table 3
ANOVAs testing the effects of female, CO_2, and their interaction on *M. menidia* offspring embryo and larval survival (logit-transformed).

Survival measure	Effect	F	df	P
Embryo	Female	9.72	4	< **0.001**
	CO_2	16.12	1	**0.001**
	Female ∗ CO_2	3.58	4	**0.023**
Larval	Female	3.59	4	**0.023**
	CO_2	0.98	1	0.333
	Female ∗ CO_2	1.68	4	0.194

Bolded P-values are significant at the 0.05 level.

Table 4
MANOVA testing for effects of female, CO_2, and their interaction on combined *M. menidia* offspring size traits (i.e., hatch length and larval length) using Pillai's Trace test statistic.

Effect	F	Hypothesis df	Error df	P
Female	4.33	8	36	**0.001**
CO_2	2.65	2	17	0.099
Female ∗ CO_2	0.83	8	36	0.581

Bolded P-values are significant at the 0.05 level.

Table 5
ANOVA testing the effects of female, CO_2, and their interaction on *M. menidia* offspring hatch length and larval length.

Measurement	Effect	F	df	P
Hatch length	Female	22.67	4	< **0.001**
	CO_2	1.74	1	0.204
	Female ∗ CO_2	0.87	4	0.500
Final length	Female	1.36	4	0.289
	CO_2	2.85	1	0.108
	Female ∗ CO_2	0.83	4	0.522

Bolded P-values are significant at the 0.05 level.

almost identical between ambient (5.3 ± 0.3 mm, 13.0 ± 1.6 mm, respectively) and acidified treatments (5.2 ± 0.3 mm, 13.7 ± 1.8 mm, respectively, Fig. 2C,D). However, for hatch length, but not final length, there were differences among females, with hatchlings of female E being on average 0.38 mm (7.4%) longer than those of female D. MANOVA on the two size traits showed significant overall effects of female ($P = 0.001$, Table 4), driven largely by the differences in hatch length (ANOVA, $P < 0.001$, Table 5), but no significant effects of CO_2 or $CO_2 * $ female (Table 4). Larvae grew at an average rate of 0.54 mm d^{-1}, and similarly, there were no significant effects of female, CO_2, or their interaction (Table 4), suggesting that offspring of different females did not exhibit differential growth responses to high CO_2 conditions (Table 5).

3.3. Fatty acids

Docosahexanenoic acid (DHA 22:6*n*3), palmitic acid (16:0) and eicosapentaenoic acid (EPA 20:5*n*3) together comprised 54% of the total FA concentration in Atlantic silverside eggs (mg dw g^{-1}), while the remaining 22 FAs contributed ~46% (electronic Supplementary material, Fig. S2). Individual FA concentrations in whole females were positively correlated ($R = 0.98$) to concentrations in unfertilized eggs, with eggs being on average 3.6 × richer in each of the 25 FAs (range: 1.1–10.5). Average egg enrichment factors varied between 2.52 × (female E) to 4.25 × (female D), but there was no significant correlation to the lnRRs of the six measured traits. Female TL was also unrelated to any of the six lnRRs. In contrast, hatch length in both the ambient and high CO_2 treatments was significantly related to cumulative FA concentrations in unfertilized eggs, and the fitted quadratic regressions explained 77% ($R^2 = 0.77$, $P < 0.001$) and 72% of the variability ($R^2 = 0.72$, $P < 0.001$), respectively (Fig. 3). Cumulative FA concentrations were inversely related to the lnRR of hatch length ($R = -0.748$, $P = 0.03$), suggesting that increasing cumulative FA levels in eggs were associated with smaller hatchlings at high compared to ambient CO_2 conditions (Fig. 3).

PCA extracted 4 PCs that explained 41%, 27%, 17%, and 14% of the variability in the FA data, respectively. Ten specific FAs showed strong positive loadings (> 0.85) on any of the 4 PCs, and six were significantly correlated to lnRRs ($P < 0.05$, Fig. 4). Levels of eicosenoic (20:1*n*9) and docosapentanoic acid (22:5*n*3) were positively related to the lnRR of embryo survival (i.e., negative CO_2 effects at low levels of both FAs), while levels of pentadecylic acid (15:0) were positively related to the lnRR of overall survival. In contrast, levels of alpha-linoleic (18:3*n*3), stearidonic (18:4*n*3), and docosahexanoic acids (22:6*n*3, DHA) were negatively related to the lnRR of hatch length (negative CO_2 effects at higher levels of these FAs, Fig. 4).

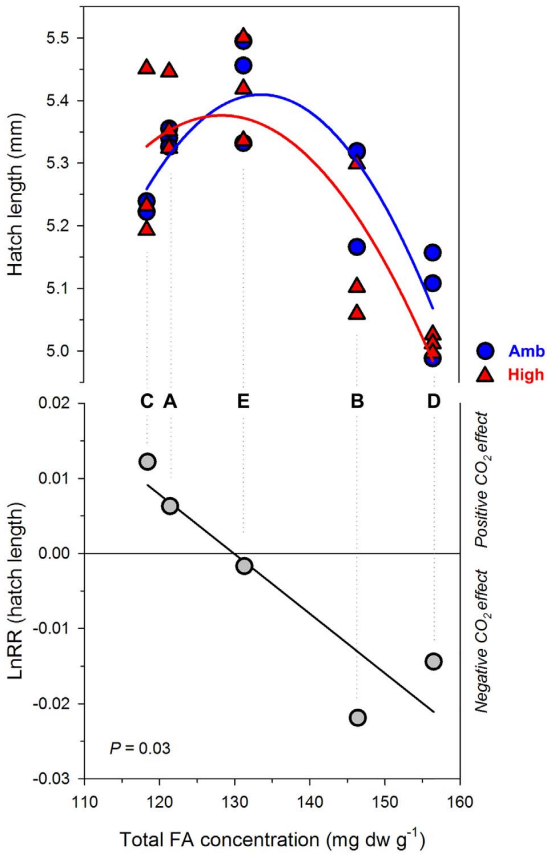

Fig. 3. *M. menidia*. Relationship between embryonic size and total fatty acid concentration in unfertilized eggs [$\Sigma(FA_{1-27})$] for offspring reared at ambient (blue circles, ~400 µatm) and high CO_2 environments (red triangles, ~2300 µatm). Upper panel shows replicate means of hatch length (mm) and total FA fitted with quadratic regressions (lines) that were both significant ($P < 0.001$). Lower panel shows log-transformed CO_2 response ratios vs. total FA fitted with a linear regression ($P = 0.03$). Letters denote females A to E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

This study examined the contribution of maternal egg provisioning and egg FA content to the susceptibility of fish offspring to high CO_2 environments. The data showed that offspring obtained from five Atlantic silverside females had variable average survival rates in response to high CO_2 conditions. Genetic and transcriptomic differences among females (Gao and Munch, 2013), as well as random effects, could plausibly account for this, however, we found that particular FAs in unfertilized eggs correlated with average CO_2 responses in offspring. This suggests that maternal provisioning, which itself could be genetically determined, may also influence CO_2 sensitivities in fish offspring.

Variable CO_2 responses in progeny from different breeding pairs have previously been documented for marine invertebrate model species such as sea urchins and mussels (Foo et al., 2016; Sunday et al., 2011) and attributed to differences in egg size and quality (Foo et al., 2016). For fish, such evidence has so far been lacking, save for incidental observations of variable survival rates in CO_2 exposure experiments; e.g., among three sib-groups of summer flounder (*Paralichthys dentatus*, 35–70%, Chambers et al., 2014). In another study, average egg survival in a tropical reef fish (*Amphiprion percula*) appeared to increase by 20% in response to high CO_2 conditions, but the authors noted that this was due to embryo batches produced by a few exceptional breeding pairs (Welch and Munday, 2016). The present study added a more comprehensive characterization of between-female variability in offspring CO_2 responses for the Atlantic silverside, an important forage fish and model in previous ocean acidification experiments.

Differential offspring responses to elevated CO_2 conditions could be adaptive for fish species like the Atlantic silverside, which spawn batches of eggs over an extended period through spring and summer in salt marshes, estuaries, and shallow embayments (Middaugh et al., 1987). These highly productive habitats often exhibit large seasonal fluctuations in oxygen and CO_2 (Gobler and Baumann, 2016), because biological productivity and community metabolism intensify during spring and summer and abate during fall and winter (Baumann and Smith, 2017; Baumann et al., 2015; Wallace et al., 2014). Hence, silverside offspring produced early in the spawning season typically encounter lower and less variable CO_2 (higher pH) conditions than individuals in the same population spawned later in the season. As demonstrated previously, this seasonal change coincides with a rapid shift from CO_2 sensitive to CO_2 tolerant silverside offspring in the wild (Murray et al.,

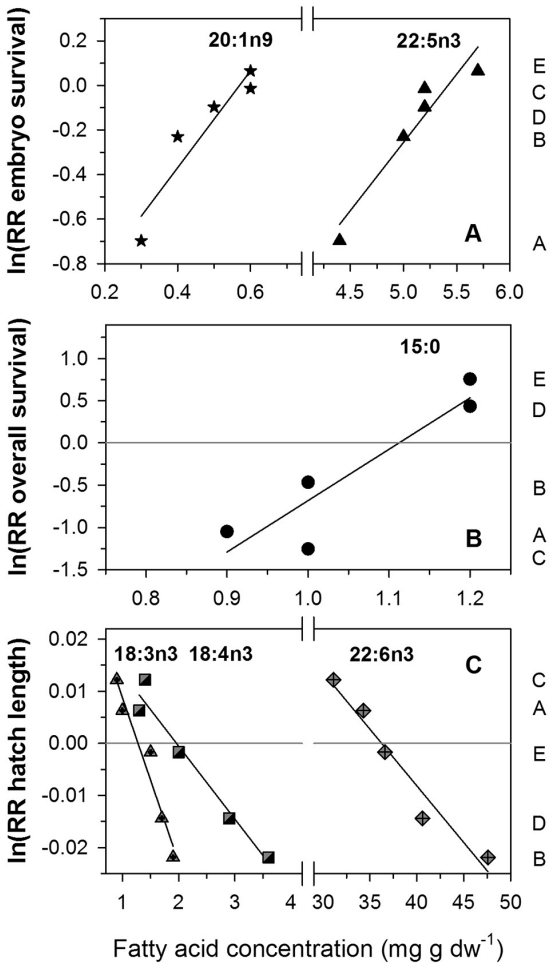

Fig. 4. *M. menidia*. Relationships between log-transformed CO_2 response ratios (lnRR) of (A) embryo survival, (B) overall survival, (C) hatch length and absolute concentrations (mg dw g^{-1}) of selected fatty acids in unfertilized eggs of five females (A–E, right side of panels). Negative (positive) lnRRs indicate a trait decrease (increase) at high CO_2 conditions.

2014), suggesting that adult spawners can precondition their offspring for the environment they are likely to encounter. While previous findings were based on average responses in offspring pooled across many spawners (> 20 females and males), this experiment followed offspring from individual females. These female (half-sib) groups differed in their CO_2 sensitivities, perhaps because conditioning does not advance uniformly among spawners in a population. Moreover, spawners used in this study were collected from the wild shortly after peak spawning season, when offspring were expected to already be largely CO_2 tolerant. This was evident when examining pooled early-life survival, which was statistically similar between ambient and high CO_2 conditions. Variability in life history traits between offspring from different mothers is likely adaptive for organisms inhabiting rapidly changing environments, which is consistent with ecological theory of the benefits of bet-hedging (Einum and Fleming, 2004; Green, 2008; Marshall and Uller, 2007). However, this has yet to be robustly applied to ocean acidification and the role of within population variability in CO_2 sensitivity (Gaylord et al., 2015).

If offspring responses to high CO_2 are partially determined by parental and particularly maternal environments (Allan et al., 2014; Miller et al., 2012), such transgenerational plasticity could be achieved via two principal pathways: epigenetic inheritance and maternal provisioning. While the first describes modifications in DNA transcription passed on to the offspring (Jablonka and Raz, 2009; Salinas et al., 2013), the second encompasses modifications of propagules, e.g., in size (Chambers and Leggett, 1996), energy content, or perhaps in specific FAs, the primary component of fish egg lipids (Wiegand, 1996). In Atlantic silversides, egg size is a relatively invariant trait (Bengtson et al., 1987) that was not measured in the present study (see also Fuiman and Ojanguren, 2011). Other potential proxies such as spawner size or overall fatty acid enrichment in eggs compared to adults were found to be unrelated to offspring CO_2 sensitivity. There was, however, a significant effect of female on size at hatch, which is consistent with previous work on this species (Gao and Munch, 2013) and the general paradigm that size variations in early life marine fish arise largely as a result of maternal effects (Chambers and Leggett, 1996; Chambers et al., 1989).

Intriguingly, a dome-shaped relationship between absolute FA levels in unfertilized eggs and the size of newly hatched larvae was found in both treatments, but these relationships differed slightly between low versus ambient CO_2 treatments (Fig. 3). The metabolic pathways responsible for these differences are presently unknown. However, the observation that several embryonic traits that were related to FA profiles is unlikely to be coincidental, because in these pre-feeding stages maternal FA provisions are not yet altered by external food sources.

A small number of specific FAs showed direct correlations to the CO_2 sensitivity of embryonic and larval traits. For example, eggs with lower concentrations of pentadecylic (15:0), eicosenoic (20:1*n*9), and docosapentanoic acids (22:5*n*3) resulted in offspring where embryo and overall survival were negatively affected by high CO_2. Since FAs in eggs essentially function as fuel and raw material for tissue and enzyme synthesis, one possible explanation therefore is that these fatty acids play a prominent role in the synthetic pathways of enzymes that determine the acid-base competency in developing embryos. Similarly, CO_2 sensitive metabolic pathways may underlie the finding that eggs with higher concentrations of alpha-linoleic (18:3*n*3), stearidonic (18:4*n*3), and docosahexanoic acids (DHA, 22:6*n*3) produced offspring where hatch length was negatively affected by high CO_2 conditions. DHA has been shown to be important in larval fish membranes, as well as being prominent in organs containing 'excitable cells,' such as eyes and other neural networks (Wiegand, 1996). Targeted ontogenetic experiments are clearly required to elucidate these potential mechanisms and to further understand the mechanistic and structural roles of individual FAs (Rainuzzo et al., 1997).

Our findings suggest that examining maternal FA provisioning of propagules will aid in developing a better mechanistic understanding of CO_2 sensitivities in fish offspring. Such approaches would build on existing evidence that variations in FA composition in eggs comprise a meaningful proxy of maternal investment, particularly in fish like the Atlantic silverside that directly allocate energy to reproduction (income breeders, McBride et al., 2015; Stephens et al., 2009). This in turn can affect critical larval traits such as antipredator performance, e.g., in larval red drum (*Sciaenops ocellatus*, Fuiman and Ojanguren, 2011), a phenomenon known as metabolic programming (Fuiman and Perez, 2015). In addition, metabolic pathways in fish embryos, larvae, and juveniles are evidently sensitive to CO_2 conditions; for example, exposure to high CO_2 has been shown to substantially alter FA profiles in larval red drum (Díaz-Gil et al., 2015) and to a lesser extent in juvenile Atlantic silversides (Murray et al., 2017). In silversides, maternal FA provisioning of propagules might therefore constitute an alternative mechanism underlying the documented seasonal shifts in offspring CO_2 sensitivity, instead or in addition to transgenerational epigenetic inheritance (Murray et al., 2014).

A central goal of CO_2 manipulation experiments is to identify sensitive life history traits in organisms as a first step towards inferring species' vulnerabilities to ocean acidification. Many issues inherent to experiments currently constrain our ability to scale these potential

responses to populations and ecosystems (Busch et al., 2015; McElhany, 2017; Pfister et al., 2014). The current study added to these challenges by suggesting that maternal provisioning and by implication, maternal environments, can influence the outcome of CO_2 exposure experiments. For example, many experiments particularly on commercially important fish species have relied on offspring produced by relatively few females (Bignami et al., 2013; Frommel et al., 2012b; Stiasny et al., 2016), whose maternal contributions may not necessarily represent population averages and thus result in overrepresentation of certain response phenotypes. Furthermore, female spawners are often derived from laboratory broodstocks (Bromhead et al., 2015; Chambers et al., 2014; Stiasny et al., 2016), where feeding and rearing conditions prior to spawning may conceivably influence maternal provisioning and thus result in offspring CO_2 sensitivities that differ from those of wild populations.

A second issue inherent to many assessments of CO_2 sensitivities in fish is their focus on single life stages such as embryos or early larvae. This study quantified embryo and larval survival across many experimental units and found that survival rates were uncorrelated between these two life stages. Our results thus caution against using CO_2 sensitivities of single life stages for broader inferences about species vulnerabilities to elevated CO_2.

A third issue highlighted by the current experiment concerns the substantial between-replicate variability in early life history traits, particularly for post-hatch survival. In this case, triplicates consisted of homogeneously distributed full- and half-sib individuals reared under meticulously controlled conditions, yet in many batches the response of one replicate sharply diverged from the other two (Fig. 2). During fish early life stages, on which CO_2 sensitivity experiments rightly focus (Baumann et al., 2012; Ishimatsu et al., 2008), offspring need to transition from endogenous to exogenous feeding, and this might be a much more stochastic process and thus greater experimental challenge than commonly acknowledged. Increased within- and between-experiment replication may be a solution; however, more work has to be done to identify replicate designs that are still logistically feasible.

The final issue highlighted by the present experiment concerns the generally positive effect of high CO_2 conditions on larval fish growth, which is consistent with a majority of studies to date on this and other fish species (Miller et al., 2012; Munday et al., 2009), but seemingly contrary to the expectation of higher metabolic demands due to increased needs for acid-base regulation. As pointed out by Murray et al. (2017), most experiments provide newly hatched larvae with excess food, which is practical but may enable high CO_2 survivors to compensate or overcompensate for increased metabolic demands by increased ingestion rates (Nowicki et al., 2012). In fish, CO_2 related additional energy demands are likely small (Esbaugh et al., 2016) but experiments administering restricted and carefully controlled food rations have detected growth reductions (Murray et al., 2017) consistent with modeled or theoretical estimates (Heuer and Grosell, 2016).

In summary, the current study suggested that individual silverside females produce offspring with varying average CO_2 sensitivities, likely due to a combination of genetic and non-genetic factors. This variability adds complexity to experimental studies aiming to elucidate the vulnerability of marine organisms to ocean acidification. While no single experiment can predict the fate of future fish populations, the accumulation of continuously improving empirical evidence is critically important to further our understanding of the consequences of a high CO_2 world for marine life.

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Conflict of interest

All authors declare no competing or financial interests.

Ethical approval

Experiments were performed under IACUC protocol #A14-032.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2017.11.002.

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